

HOUSE WRENS ADJUST LAYING DATES AND CLUTCH SIZE IN RELATION TO ANNUAL FLOODING

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ABSTRACT.—I examined timing of reproduction and productivity in box-nesting House Wrens (*Troglodytes aedon*) inhabiting three riverbank woodlands subjected to different levels of flooding. In years when the North Platte River flooded its banks submerging ground foraging substrates, dates of nest initiation and egg laying in two wren populations were delayed and nonsynchronized. In contrast, timing of breeding was unrelated to annual variations in water levels or spring weather in wrens occupying a riparian area buffered from flooding. Rates of nest predation were unlikely to influence timing of laying because they did not vary among years or between early and late nests in any locality. Initial clutch size declined seasonally in all populations and was smaller in years when breeding was delayed by flooding. At all localities, variation in numbers fledged from successful nests was related to interactions between year and laying date. Generally, more nestlings fledged from early nests because clutches were larger. In addition, early clutches lost fewer young than late clutches of equal size in the population most impacted by flooding. Greater fledging success may select for early laying and may explain higher laying synchrony in early years. *Received 15 Jan. 1990, accepted 27 Aug. 1990.*

The seasonal onset of breeding in birds is often delayed by unfavorable environmental conditions (Lack 1966). Average laying dates in many bird species shift from year to year in response to annual variations in spring temperatures (van Balen 1973), snow melt (Slagsvold 1976, Zwickel 1977, Hannon et al. 1988), wetland dryness (Davies and Cooke 1983, Afton 1984), and food availability (Kallander 1974, von Bromssen and Jansson 1980, Ewald and Rohwer 1982). Average clutch size is often smaller in years when the breeding season starts late (Perrins 1970, Murphy 1986, Perrins and McCleery 1989), and clutch size also typically declines in individuals within years as the breeding season progresses (Klomp 1970, Perrins 1970, Hussell 1972, Murphy 1986, Svensson 1986). Diverse relationships between clutch size and timing of reproduction have been documented (e.g., Bédard and LaPointe 1985, Dickinson et al. 1987), but few studies have examined the effects that unpredictable catastrophic events have on egg-laying dates and clutch size.

House Wrens (*Troglodytes aedon*) are abundant breeders in deciduous riverine woodlands of the north-central Rocky Mountains (Finch 1989a). Such riverbank woodlands experience spring flooding annually, with water

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flow levels that vary greatly from year to year. Periodic flooding can have a major impact on associated plant and animal communities (Ewel 1979, Hunter et al. 1987), on use of foraging habitats by birds (Powell 1987), and on abundance, breeding time, and reproductive success of bird species that feed or nest on the ground (Knopf and Sedgwick 1987, Cruz and Andrews 1989, Ohlendorf et al. 1989). House Wrens glean insect prey off substrates near the ground (Guinan and Sealy 1987, 1989), and habitat selection by wrens may be related to availability of foraging substrate near nest sites (Guinan and Sealy 1989). The submergence of foraging substrates and food supplies under high floodwaters of long duration is a severe disturbance that may affect timing of reproduction in House Wrens.

Box-nesting House Wrens were studied over a four-year period in three woodland areas exposed to different levels of flooding. Here, I compare spatial and annual variations in timing of nest building and egg laying in wrens to variation in water flow levels, climatic factors, and rates of nest predation. To determine if productivity was associated with egg-laying dates, I tested for differences in clutch size and rates of fledging between early and late nests.

STUDY AREA AND METHODS

Three study plots were established in May 1982 in streamside habitats in Carbon County, southeastern Wyoming, at elevations ranging between 2050 and 2250 m. One plot was established at Rock Creek, 5 km northeast of Arlington and about 70 km northeast of Saratoga, and two plots, named Foote Camp and Treasure Island, were spaced 34 km apart along the North Platte River near Saratoga. Woodlands on the three study plots were dominated by narrowleaf cottonwood (*Populus angustifolia*); a variety of shrub species, especially willows (*Salix* spp.); and herbaceous species. Shortgrass prairie interspersed with sagebrush (*Artemisia* spp.) bordered riparian woodlands. Vegetation composition of the study plots is described in greater detail in Finch (1989b).

The extent of flooding varied among plots and years. The proportion of nest-box sites (21–22 boxes/plot) surrounded by floodwater was used as an index to the amount of ground surface covered. Foote Camp, the plot at the lowest elevation (2050 m), experienced heavy overbank flooding by the North Platte River in 1983 and 1984, and less so in 1986, with water covering as much as 100% of the ground surface for up to three weeks. The Foote Camp plot had gradual bank slopes and was bounded on three sides by a forked river, which may in part explain high river overflow. Treasure Island, also on the North Platte River, was flooded with less water (about 30% of the plot's surface was submerged in 1983 and 1984, and about 15% in 1986) for a shorter duration, probably because the riverbank was high (1.5–2 m) and on one side of the study plot only. Rock Creek, a smaller stream at the highest elevation (2250 m), flooded in 1983, 1984, and 1986, covering 0–15% of the plot's surface with water during peak flows. The Rock Creek plot was 120 m west of the stream and was buffered from water overflow by a strip of land. Rock Creek was used as a regulated irrigation channel, and level of water flow was erratic throughout each spring and summer, reflecting amounts of dam discharge in addition to runoff levels.

Nest boxes on all three plots were mounted 2 m high on live deciduous trees >10 cm dbh. The sample size of boxes on each plot was limited by woodland size. Boxes were spaced

at 30–35 m intervals in grids conforming to the shape and size of the riparian corridor. Nest boxes were built of 1.7-cm-thick cedar, $14 \times 14 \times 28$ cm in dimension, with 3.8-cm-diameter entrances and latchable top doors.

Status (empty or occupied) of box and progress of nesting attempts were determined by checking all nest boxes early in the afternoon every 2–4 days from mid-May to late August of 1983 through 1986. Only a few boxes were used by wrens twice during a single breeding season. Boxes were cleaned out at the end of each summer so that nests from prior years were not mistaken for new nests. Because individual male House Wrens frequently fill multiple cavities with twigs (Kendeigh 1941), the appearance of the first egg was used as an index to nesting. For true nests, the first appearance of nesting material was identified as the date of nest initiation. Dates of nest initiation and egg laying were converted to numbers of days after May 1. The number of days between the egg-laying date and the nest-initiation date was considered the period of nest construction. Effects of the two factors, YEAR (1983, 1984, 1985, 1986) and PLOT (Foote Camp, Treasure Island, Rock Creek), were determined using two-way ANOVA's to test for temporal and spatial differences in dates of egg laying. The standard error of egg-laying date was used as an index of nesting synchrony. With regard to those boxes used twice in the same season, "second" nesting attempts were excluded from ANOVA's of egg laying because box reuse by the same pair of unmarked House Wrens could not be distinguished from late box settlement by a new pair.

Total annual precipitation, and mean minimum, mean maximum, and overall temperatures in May of each study year were computed from meteorological data collected at Saratoga, located 13 km southeast of the Foote Camp plot and 21 km northwest of the Treasure Island plot, and at Elk Mountain, 14 km northeast of the Rock Creek plot. Topography was relatively constant between field sites and matching weather stations, and therefore, I am confident that weather data at stations reflected weather at study plots. In contrast, even though the Elk Mountain and Saratoga weather stations were only about 60 km apart, temperature and precipitation data varied between stations owing to differences in elevation, slope exposure, and proximity to mountains. Water flow was measured at two stations: North Platte River above Seminoe Reservoir, near Sinclair, Wyoming, and Rock Creek above King Canyon Canal, North Arlington, Wyoming. Total flow levels (ha-m) and midweekly flow rate (m^3/s) from April to September of 1983 through 1986 are reported. Weather and water flow data were collected by Wyoming Water Research Center, Univ. of Wyoming, Laramie.

Because flood levels and weather factors varied by year, their effects may explain year-to-year variation in onset of reproduction. I ranked yearly weather data and water levels from high to low and compared these scores to mean annual dates of egg laying using Spearman's rank correlations (coefficients are labeled r_s) (Sokal and Rohlf 1981).

Reproductive outcome, a dichotomous variable (failure or success), was classified as successful if at least one offspring fledged from the nest. Nests were considered abandoned if adults no longer attended the nest, and nest contents failed to hatch or fledge. Predation of whole clutches or broods was assumed if nests were empty before nestlings were due to fledge. Partial losses of clutches and broods resulted from egg-puncturing by intruders (probably other wrens; Kendeigh 1941; Belles-Isles and Picman 1986a, b; Freed 1986), hatching failure, and nestling starvation. Nests with reduced broods were considered successful if the remaining nestlings fledged. The difference in mean initial clutch size between successful and failed nests was assessed using ANOVA with the factors YEAR, PLOT, and OUTCOME entered concurrently.

Egg destruction by conspecifics and predation were the major causes of nest failure, accounting for 89% of 27 unsuccessful attempts (Finch 1990). I divided egg-laying dates into early and late periods and used contingency tables (OUTCOME \times laying period) to

determine if frequency of nest destruction was dependent on timing of reproduction. Early and late periods were defined as dates before and after the mean date of egg laying each year for each stream. Outcome data from different years were combined if they were homogeneous or analyzed separately if they were heterogeneous.

To estimate timing and extent of brood losses, numbers of offspring fledged from each successful nest were subtracted from its initial clutch size. Wren clutches of unknown initial size were excluded from mean estimates of numbers fledged and lost from successful nests. To test for temporal and spatial variation in clutch size after egg laying and fledging, I analyzed the main and interaction effects of YEAR and PLOT using two-way ANOVA's. I also used two-way ANOVA's with factors YEAR or PLOT (depending on homogeneity of data), and laying period (early and late), to determine if clutch size, or numbers and rate (% clutch) that fledged, were related to timing of reproduction. To interpret seasonal changes in clutch size, pairwise comparisons among years were computed using Tukey's range test. I removed the effects of the factors PLOT and YEAR by computing case-wise residuals (listed by the MANOVA procedure, SPSS/PC+) and then used linear regression analysis to evaluate relationships between the residuals of laying date and the residuals of each dependent variable—initial clutch size of all nests, clutch size of successful nests, or numbers and percent of offspring fledged. To detect shifts in clutch size and fledging success with seasonal progression in laying dates, all early and late nesting attempts were included in analyses of clutch size and productivity.

All statistical analyses were performed using SPSS/PC+ programs (Norusis 1988a, b). A 0.05 probability level was used to test main effects and a 0.25 level to evaluate interaction effects in all applicable ANOVA's (Bancroft 1968). In tests with two or more factors, each effect was adjusted for all other factor effects using the default option, "classic experimental approach," in Procedure ANOVA. In analyses where interactions of PLOT and YEAR potentially masked relationships, I used one-way ANOVA's (or *t*-tests for pooled data) to reveal variation in laying dates, clutch size, or numbers fledged among plots by year or among years by plot.

RESULTS

Factors Affecting Dates of Egg Laying

Year and plot.—House Wrens generally began building nests in boxes later in 1983 and 1984 than in 1986 and, especially, 1985 (Fig. 1). Mean dates of nest initiation were earliest in 1985 on all three study plots, with the earliest nest found on 17 May 1985 at Foote Camp. Mean period of nest building in House Wrens ranged from a high of 13.3 ± 5.1 days at Treasure Island in the first study year to a low of 5.0 ± 0.3 days at Treasure Island in 1986. The earliest clutch found during the 4-year period was initiated on 22 May 1985. Variation in mean date of egg laying (after May 1) reflected the variation in mean date of nest initiation (Fig. 1). To eliminate problems associated with analyzing correlated variables (Beal and Khamis 1990), I report statistical comparisons of egg-laying dates only.

Mean laying dates varied among years ($F_{3,75} = 9.66$, $P < 0.0001$, $N = 87$) but not among plots ($F_{2,75} = 2.70$, $P = 0.075$). Based on results of one-way ANOVA's, annual laying dates varied at Foot Camp ($F_{3,22} =$

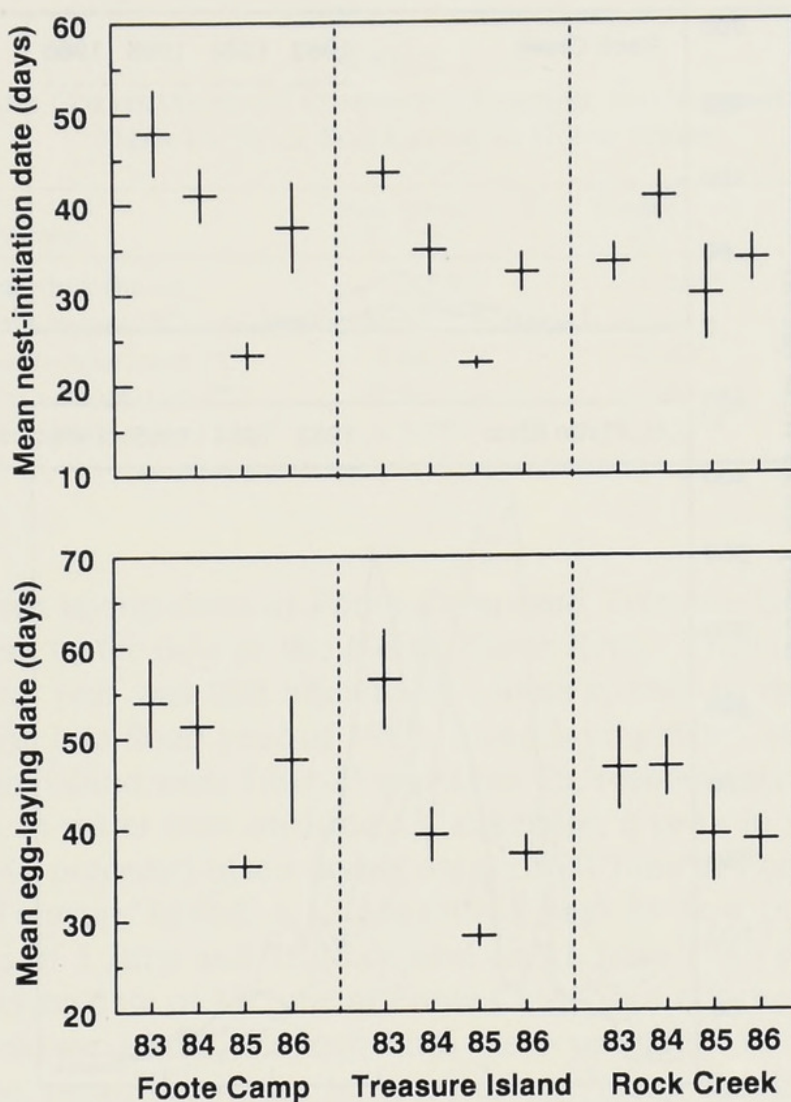


FIG. 1. Mean dates (\pm SE) of nest initiation and egg laying from 1983 through 1986 in three populations of House Wrens. Dates are days after May 1.

5.97, $P = 0.004$) and at Treasure Island ($F_{3,22} = 8.13$, $P = 0.001$) but not at Rock Creek ($F_{3,22} = 1.28$, $P = 0.297$). The importance of PLOT main effects may have been masked by the interaction of PLOT and YEAR ($F_{6,75} = 2.08$, $P = 0.066$). By analyzing plot variation by year, differences in mean laying dates among plots were exposed (one-way ANOVA: $P < 0.05$). Directional trends in mean laying dates were similar between the two plots on the North Platte River (Fig. 1), but these trends did not resemble the annual pattern in laying dates at Rock Creek.

Flooding and weather.—Declines in mean dates of laying from 1983 through 1985 were apparent in the North Platte River areas (Fig. 1). Laying dates were earliest at Foote Camp and Treasure Island in 1985, which may be related to low water levels of the North Platte that spring (Fig. 2). Water flow of the North Platte River was lowest in 1985, and

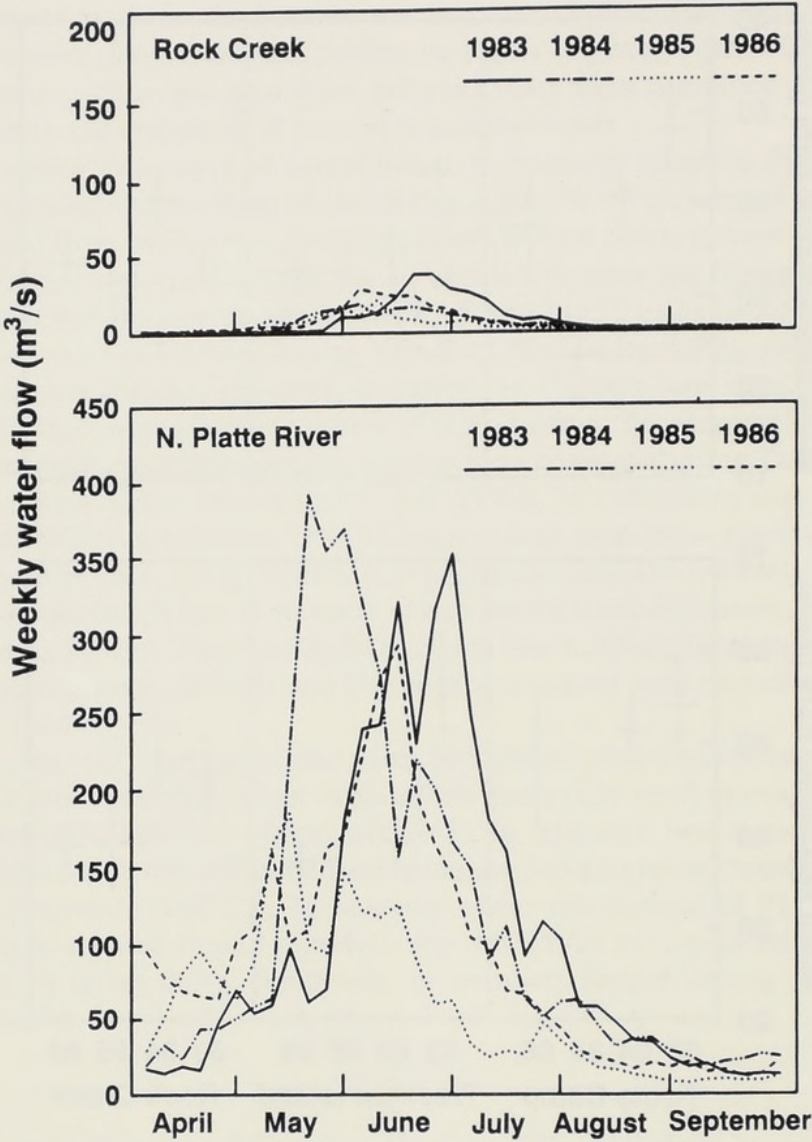


FIG. 2. Weekly water flow (m³/s) from 1983 through 1986 of two streams adjacent to woodlands used by breeding House Wrens.

the two plots on the North Platte did not experience the heavy floods typical of the other three study years. In contrast, total water flow of the North Platte and Rock Creek peaked in 1983, the first study season. Some of the latest clutches on all three study plots were laid in 1983. However, wrens may have delayed egg laying in 1983 if this first study year was a transition period for learning about and adapting to nest boxes (see Finch 1989b). Nevertheless, water levels of the North Platte were also high in 1984 and less so in 1986, and again, egg laying at Foote Camp and Treasure Island was later than that in 1985.

Mean dates of egg laying (ranked by year) at Foote Camp and Treasure Island were perfectly and positively correlated ($r_s = 1.0$) with level of water flow of the North Platte River, but timing of nesting at the Rock Creek plot was not related to water levels of Rock Creek (Table 1). In

TABLE 1

SPEARMAN RANK CORRELATIONS (r_s) COMPARING WEATHER AND WATERFLOW FACTORS TO MEAN DATES OF EGG LAYING IN HOUSE WRENS

Variable	Foote Camp (N = 4)	Treasure Island (N = 4)	Rock Creek (N = 4)
Total waterflow (ha-m)	1.00**	1.00**	0.00
Mean temperature (°C)	-0.40	-0.40	0.40
Minimum temperature (°C)	-0.40	-0.40	0.20
Maximum temperature (°C)	-0.80	-0.80	0.40
Total precipitation (cm)	1.00**	1.00**	0.40

** $P < 0.005$.

general, mean laying dates at Foote Camp and Treasure Island followed dates of peak water flow of the North Platte River. That is, the average clutch in any year was laid after flood waters started to recede. For example, in the late flood year of 1983, mean laying dates at Foote Camp and Treasure Island were June 23 and June 26, respectively, following an initial peak in water flow on June 13. Likewise, a peak in water flow on 26 May 1984 preceded mean laying dates of 20 June at Foote Camp and 4 June at Treasure Island; a 12 May 1985 peak in flow preceded mean laying dates of 5 June and 26 May; and an 11 June 1986 peak preceded the mean laying date of 17 June at Foote Camp, but not the 6 June laying date at Treasure Island. Laying dates were unrelated to overall mean temperature, mean minimum temperature, or mean maximum temperature at any plot (Table 1).

Standard error in the date of clutch initiation was positively correlated with mean laying date at the Platte River plots ($r_s = 0.86$, $P < 0.001$, $N = 8$), indicating higher synchrony in low-flood years when nesting was early. Timing of reproduction at Rock Creek was generally less consistent within each breeding season than at the Platte River plots (Fig. 1), and standard error in laying dates was unrelated to mean laying date at this plot ($r_s = 0.20$, $P > 0.05$, $N = 4$). Caution should be used in interpreting the lack of a relationship between laying dates and standard errors at Rock Creek because the standard errors for any given year at Rock Creek may have been influenced by small sample size.

Timing of reproduction at plots on the North Platte River was also positively related to total annual precipitation (Table 1). Flood levels correspond to levels of spring runoff from snowmelt which are closely linked to total precipitation (i.e., amount of snowpack). Flood levels were perfectly and positively correlated to total precipitation at the North Platte River ($r_s = 1.00$, $P < 0.01$, $N = 4$). If precipitation rather than flooding

influenced timing of reproduction at the North Platte River plots, then onset of breeding should similarly be related to precipitation at the Rock Creek plot which was buffered from flooding (i.e., results are not confounded by flood effects). But mean dates of egg laying at Rock Creek were not associated with total precipitation (Table 1). Therefore, the relationship between delayed reproduction and increased precipitation at the Platte River plots may be an incidental outcome of the relationship between flood levels and precipitation.

Relationship Between Timing of Reproduction and Productivity

Frequency of nest failure.—Rates of nest failure were similar among years at each study area ($P > 0.05$) but differed among plots ($\chi^2 = 8.6$, $df = 2$, $P = 0.014$) so data were combined across years and analyzed by plot. The probability of nest destruction was greater at Foote Camp (44.4% of 27 nests) than at Treasure Island (8.0% of 25 nests), but both these probabilities were not statistically different from that at Rock Creek (30.6% of 36 nests). Early nests were lost at comparable rates among areas ($P > 0.05$), but late nests were more likely to fail at Foote Camp than at the other plots ($\chi^2 = 5.7$, $df = 2$, $P = 0.05$). At each plot, however, early nests were as likely to be destroyed as late nests ($P > 0.05$).

Initial clutch size.—Initial clutch size in House Wrens ranged from 3 to 10 eggs with an overall mean (\pm SD) of 6.2 ± 1.5 ($N = 93$) and a mode of 6 (33% of 93). Mean clutch size was similar among woodlands ($F_{2,81} = 2.41$, $P = 0.096$) but varied by year ($F_{3,81} = 3.68$, $P = 0.015$), reaching a maximum seasonal average of seven eggs at the Platte River plots in 1985 (Table 2), the year of minimum flooding. Main effects of plot may

TABLE 2
MEAN CLUTCH SIZE OF HOUSE WRENS LAYING EARLY AND LATE EACH YEAR ALONG TWO STREAMS

Laying period	N	1983		1984		1985		1986	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
North Platte River									
Early	28	7.3	1.5	5.6	1.3	7.0	1.5	5.8	1.2
Late	27	4.0	0.9	5.3	0.8	7.0	1.0	5.3	2.2
Total	55	5.7	2.1	5.4	1.0	7.0	1.2	5.6	1.5
Rock Creek									
Early	24	7.2	1.1	7.1	1.4	7.2	0.8	6.0	1.2
Late	14	6.3	1.2	5.5	0.6	6.3	0.5	6.0	1.7
Total	38	6.9	1.1	6.6	1.4	6.8	0.8	6.0	1.3

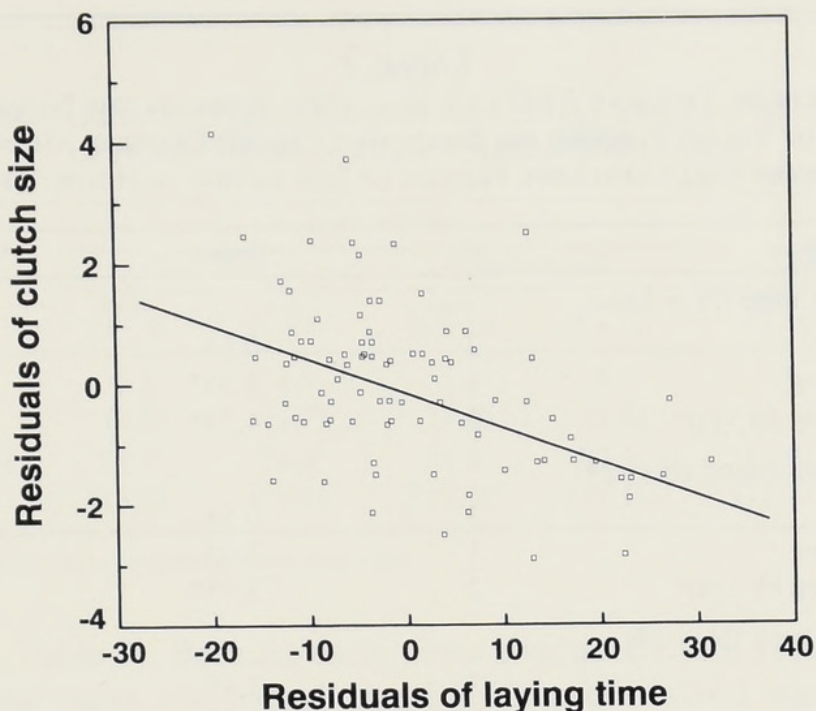


FIG. 3. Relationship between residuals of clutch size and residuals of laying time in House Wrens after PLOT and YEAR effects were removed.

have been masked by interactions between PLOT and YEAR ($F_{6,81} = 1.65$, $P = 0.145$). In within-year comparisons, however, clutch size did not differ between the two Platte River plots (t -tests by year: $P > 0.05$).

To test the relationship between clutch size and laying period, the homogeneous data from the two Platte River plots were combined and analyzed separately from the Rock Creek data. Overall mean clutch size (adjusted for YEAR effects using ANOVA) varied between early and late clutches in House Wrens along the North Platte River ($F_{1,47} = 8.49$, $P = 0.005$). Interactions between laying time and YEAR affected clutch size at the North Platte River plots ($F_{3,47} = 4.70$, $P = 0.006$), with early clutches having more eggs than late clutches in 1983 and 1986 (Tukey's test: $P < 0.05$), but not in 1984 and 1985 (Table 2). At Rock Creek, early clutches were generally larger in size than late clutches ($F_{1,30} = 5.08$, $P = 0.032$) (Table 2), but interactions between laying period and YEAR were not significant ($P > 0.25$). When nests from different plots were pooled, the relationship between residuals of clutch size and laying dates (YEAR and PLOT effects removed) was negative ($r = -0.44$, $P < 0.0001$, $N = 93$) (Fig. 3).

Mean clutch size was 5.6 ± 1.5 eggs in failed nests (failure: 26% of 93 nests), and 6.4 ± 1.4 eggs in successful nests (success: 74% of 93). Successful nests had larger initial clutches than those that failed ($F_{1,72} = 13.07$, $P = 0.001$) (adjusted for PLOT and YEAR effects). Clutch size residuals

TABLE 3

F-VALUES FROM TWO-WAY ANOVA'S INDICATING WHETHER THE NUMBERS AND PERCENTAGES OF YOUNG FLEDGED PER SUCCESSFUL CLUTCH DIFFERED AMONG YEARS AND BETWEEN EARLY AND LATE PERIODS OF EGG LAYING IN HOUSE WRENS

Factor	df	Fledged	% Fledged
Foote Camp (N = 16)			
Year	3	0.69	1.39
Laying	1	8.55*	6.85*
Laying by year ^a	3	4.23*	6.15*
Treasure Island (N = 24)			
Year	3	0.54	1.57
Laying	1	3.03	2.10
Laying by year ^a	2	3.95*	5.29*
Rock Creek (N = 29)			
Year	3	2.46	1.90
Laying	1	1.27	0.23
Laying by year ^a	3	3.00*	0.76

* $P < 0.05$.

^a Interaction effects.

(YEAR and PLOT effects removed) were negatively related to laying time in successful nests ($r = -0.52$, $P < 0.0001$, $N = 71$), whereas clutch size and laying time were not associated in failed nests ($r = -0.35$, $P = 0.117$, $N = 21$). In sum, successful clutches were larger in initial size than failures, and these larger clutches were laid earlier in the season.

Successful fledging. — The number of young fledged from each successful nest ranged from two to eight wrens with a mean (\pm SD) of 5.2 ± 1.5 (358 of 440 eggs, 81%). Numbers fledged per successful nest were similar among years and in PLOT by YEAR interactions ($P > 0.25$) but varied by PLOT ($F_{1,46} = 4.84$, $P = 0.033$, $N = 69$). Fledging rate (% fledged/clutch) varied by PLOT ($F_{1,46} = 10.24$, $P = 0.002$) but was not affected by YEAR, or by PLOT by YEAR interactions ($P > 0.25$).

Although more young fledged ($r = -0.27$, $P = 0.025$) from earlier nests (residuals analyzed after PLOT and YEAR effects were removed using MANOVA), laying date explained only a small percentage of the total variation in numbers fledged (7%). Because offspring production from successful nests differed among plots, I analyzed data from each plot separately to determine if the relationship between productivity and laying date varied among plots. Because sample sizes were small per plot-year, these results should be regarded with caution. The influence of laying date on fledging success varied by year at Treasure Island (laying by YEAR

TABLE 4
MEANS AND PERCENTAGES OF YOUNG FLEDGED FROM EARLY AND LATE SUCCESSFUL NESTS
OF HOUSE WRENS IN THREE RIVERINE WOODLANDS

Measure of productivity	North Platte River				Rock Creek	
	Foote Camp		Treasure Island		Early (N = 18)	Late (N = 11)
	Early (N = 8)	Late (N = 8)	Early (N = 13)	Late (N = 11)		
Fledge	5.5 (0.8) ^a	4.6 (1.7)	5.0 (1.3)	4.1 (1.8)	5.9 (1.3)	5.6 (1.2)
Percent fledged	78.7 (13.3)	74.8 (19.4)	81.4 (19.5)	77.9 (17.1)	83.9 (12.2)	87.9 (14.1)

^a Standard deviations are in parentheses below each mean.

interaction, Table 3). Because early nests produced more young than late nests in some years, the overall trend at Treasure Island was a seasonal decline in fledging success (Table 4). Numbers fledged at Rock Creek displayed a similar trend (Table 4) and were also affected by interactions between laying date and YEAR (Table 3). At Foote Camp, however, numbers and percent that fledged varied between early and late nests (Table 3) with early nests producing more young (Table 4). The influence of laying date on fledging success at Foote Camp was also dependent on the year that the clutch was laid (laying by YEAR interaction, Table 3).

Clutch size in successful nests (plots and years pooled) was positively associated with the number of wrens that fledged ($r = 0.73$, $P < 0.0001$, $N = 69$). Hence, early clutches at Foote Camp produced more fledglings than late clutches because early clutches were larger. However, the relationship between clutch size and numbers fledged was stronger at Treasure Island ($r = 0.73$, $P = 0.0001$, $N = 24$) and Rock Creek ($r = 0.76$, $P < 0.0001$, $N = 29$) than at Foote Camp ($r = 0.57$, $P = 0.022$, $N = 16$). Because fledging rate was not correlated with clutch size at Foote Camp ($r = -0.11$, $P = 0.685$), the negative main effect of laying date on fledging rate detected at this plot only was independent of the collinearity between clutch size and numbers fledged.

Tests of the effects of laying date on rates of partial losses (% losses/clutch) were interchangeable, i.e., they generated the same statistical values, as tests of laying date effects on fledging rates. The average number of eggs or nestlings lost from nests that otherwise survived was 1.2 ± 1.1 offspring per clutch (83 of 440 eggs, 20%). Partial losses were absent at 21 successful nests, whereas three clutches were reduced by as many as four young (maximum lost: 67% of initial clutch). Reductions were higher (68 of 83 losses, 82%) during the incubation (plus hatching) period than

during the nestling stage. Also, in nests that remained active to fledging, larger clutches lost more young than smaller clutches ($r = 0.32$, $P = 0.008$, $N = 69$) (pooled across plots and years). Hatching failure and egg destruction by conspecifics accounted for most egg losses (Finch 1990), while nestling losses were due to starvation of young and predation during the time of fledging.

DISCUSSION

Timing of Reproduction

Mean dates of egg laying varied among years in House Wrens inhabiting woodlands along the North Platte River, but not in wrens occupying the Rock Creek area. Timing of reproduction on the North Platte River was strongly correlated with annual variations in levels of water flow of the North Platte. Overbank flooding of the North Platte occurred in years of high total precipitation, resulting in submergence of wooded land surfaces. Wrens forage on substrates near the ground (Guinan and Sealy 1987, 1989), and in this study, nested later in years when floodwaters rose in May and June, covering foraging substrates. Levels of water flow did not influence timing of reproduction at the Rock Creek site where overbank flooding was absent or minor compared to the North Platte River because of smaller stream size and greater distance of the stream from the nest boxes.

The peak period of water flow (mid-May to early July) overlapped the time when wrens were constructing nests, incubating eggs, and feeding nestlings. Annual and seasonal changes in water flow rates and water levels may directly influence availability, abundance, and hatching phenology of emergent insect prey. In heavy flood years, wren egg laying may be delayed if food shortages inhibit clutch formation, if nest sites are submerged under water, or if nest sites are unsuitable because adjacent habitat is flooded. As a consequence of late nesting, offspring will fledge in late July and August, when ground surfaces are drier and accessible for foraging, and drowning risks to offspring are reduced. On average, House Wrens along the North Platte River laid clutches in any year after seasonal peaks in water flow when flood waters began to recede. Hence, in areas where overbank flooding is severe and episodic, progressive seasonal rises and falls in water levels may serve as salient environmental cues for predicting the suitable time to breed.

Laying time was more synchronized along the North Platte River in 1985 when flooding was absent. Synchronized laying by many bird species may be common in years when early breeding is possible (e.g., Murphy 1986; Fig. 3, Hannon et al. 1988). The influences of other factors on

timing of egg laying were apparently more uniform and presumably more important than effects of flooding absence, allowing simultaneous early nesting by wrens in 1985. For example, early spring phenology as indexed by "warmth sums" (sum of number of degrees that mean temperatures reach above zero) is likely to favor early laying (Kluijver 1951, 1952; Murphy, pers. comm.), especially in years when potential impacts of disturbance factors are negligible. Local conditions may be more heterogeneous in years of heavy flooding if some habitat patches become suitable earlier than others. Also, response time may differ among females as flood waters recede if some are younger or less experienced in judging environmental conditions and the time to lay (Middleton 1979, Nol and Smith 1987), if body condition or fat reserves vary, or if a genetic component dictates timing of laying (Van Noordwijk et al. 1981).

Nest Failure, Clutch Size, and Fledging Rates

Nest predation increases through the breeding season in some bird species (Robertson 1973, Wiklund 1984) and declines over time in others (Findlay and Cooke 1982). It also varies from year to year (Myrberget 1986, Hannon et al. 1988) and from site to site (Murphy 1983, Picman 1988, Rotenberry and Wiens 1989). In this study, the probability of House Wrens fledging one or more young per nest varied significantly among riparian woodlands, but not among years. The frequency of nest failure did not differ between early and late nests at any plot, and therefore predation rates probably did not influence timing of breeding in House Wrens. Nest destruction by mammals, conspecifics, and possibly snakes was greatest at Foote Camp, the site where box occupancy rates were highest (Finch 1990), and late nests were more likely to fail at this site than at Rock Creek or Treasure Island. Seasonal and annual variation in predation rates may be more common when predators are abundant (e.g., Hannon et al. 1988), when predator or prey densities vary (e.g., Findlay and Cooke 1982, Angelstam et al. 1985), or when changes in plant phenology and habitat structure affect search efficiency of predators (e.g., Bowman and Harris 1980) or defense capability of prey.

Birds that lay early often have larger clutches than those that breed later in the season (Klomp 1970, Harvey et al. 1985, Murphy 1986). In this study, House Wrens laid larger clutches earlier in the breeding season in both geographical areas. Finke et al. (1987) also reported a seasonal decline in clutch size of House Wrens. My data were not sufficient, however, to test for the factors affecting within-season variation in clutch size. Clutch size may decline with season when individual females differ in age or experience (Curio 1983, Nol and Smith 1987), body mass or physical condition (Jarvinen and Vaisanen 1984), or genetic schedules (Van

Noordwijk et al. 1981). Individuals may adjust clutch size in response to seasonal and spatial heterogeneity in competition (Stutchbury and Robertson 1988), food supply (Greenlaw 1978, Hogstedt 1981), or territory quality (Hogstedt 1980), thus safeguarding their own chances of survival (Moss et al. 1981) while satisfying the feeding demands of their offspring (Perrins and Moss 1974, Nur 1986).

Late-nesting House Wrens with experimentally enlarged broods can raise additional chicks that weigh the same as those in broods of modal size (Finke et al. 1987). If offspring do not differ in survivorship before fledging as Finke et al. maintain, then House Wrens may adjust clutch size in relation to the probability of offspring survival after young leave the nest. Drilling and Thompson (1988) demonstrated that rates of return to natal sites were higher for House Wren chicks from early nests than for those from late nests. House Wrens fledging late have less time to develop, molt, acquire nutrient reserves, and learn survival skills before fall migration. A short developmental period before migration may explain reduced overwinter survival and lower recruitment rates of late-hatching chicks (Drilling and Thompson 1988, Hepp et al. 1989). To offset a seasonal decline in success resulting from low survival rates of late-fledging offspring, adult females may limit clutch size late in the season or in late years.

Mean clutch size fluctuates annually with mean laying date in populations subjected to environmental conditions that vary from year to year (Murphy 1986, Perrins and McCleery 1989). Spring weather and food supply are the extrinsic factors most frequently implicated as causes of yearly variation in breeding time and productivity of passerines (Perrins 1970, Hussell 1972, van Balen 1973). In this study, House Wrens along the North Platte River varied clutch size among years in relation to yearly shifts in laying schedules. In years when the North Platte River flooded its banks, laying was delayed and mean clutch size was smaller. In contrast, in the year when flooding was absent, clutches were large in both early and late nests apparently because late nests were earlier relative to other years. At Rock Creek, mean clutch size was similar among years, corresponding to the annual constancy in mean laying dates and the lack of flooding effects. Annual variation in clutch size in House Wrens may be related to year-to-year variability in conditions suitable for offspring survival, such that larger clutches are selected against in unfavorable years, e.g., late years of heavy flooding.

Laying larger clutches as early as environmental conditions allow has advantages for House Wrens. More nestlings fledged from early nests at Foote Camp, the plot most impacted by yearly variation in flooding. At all localities, seasonal differences in fledging success varied by year. In

years of delayed breeding, late nests produced fewer fledglings than early nests. Greater fledgling production was related to larger clutch size in early nests as well as to reduced rates of brood reduction. Rates of partial losses were less at early nests than at late nests, and as a consequence, early clutches fledged more young than late clutches of equal size. This may select for early laying and may explain the higher synchrony in laying dates observed at the North Platte River in early years.

Annual and within-season flooding inundates land surfaces with variable amounts of water which may affect food supply, food acquisition and delivery to young, and parenting abilities. Partial losses were caused by nestling starvation, egg destruction, and hatching failure. Seasonal changes in hatching failure may be related to variation in egg quality (Jarvinen and Väisänen 1983, 1984) resulting from seasonality in food value or availability, and physical condition of females. Increased rates of clutch/brood reduction later in the season may be associated with reduced food supplies (e.g., Hogstedt 1981) or early onset of winter weather. Also, late-nesting females are often young and inexperienced and may not be able to forage efficiently enough to produce high quality eggs or provision all their young (Perrins and Moss 1974, DeSteven 1978).

In my study areas, yearly fluctuation in flood levels appeared to be the most important extrinsic factor inhibiting the onset of reproduction in House Wrens. The catastrophic effects of flooding may have overshadowed the influences of other extrinsic factors. Alternate factors may operate more strongly in years when levels of water flow are low. Also, this study did not evaluate how intrinsic differences among individual females or males affect laying time or productivity. More data are needed to determine such effects. In this study, three populations of House Wrens responded to local and geographical variations in environmental conditions each year by adjusting laying date and clutch size. When environments are temporally variable and locally unpredictable, organisms may adjust reproductive effort relative to the probability of reproductive success (Williams 1966). Flexibility in reproductive effort, habitat use (Finch 1989a), and nest-site selection (Gutzwiller and Anderson 1987, Finch 1989b), as well as behavioral dominance in interspecific interactions (Belles-Isles 1986a, Finch 1990) may explain why House Wrens numerically dominate avifaunas in deciduous woodlands of the Rocky Mountains (Finch 1989c, Finch and Reynolds 1988).

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